Aquatic Botany 155 (2019) 25–31

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Effects of salinity and light on growth and interspecific interactions between *Myriophyllum spicatum* L. and *Ruppia maritima* L.

Eva R. Hillmann[a], Megan K. La Peyre[b,*]

[a] School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, United States
[b] U.S. Geological Survey, Louisiana Fish and Wildlife Cooperative Research Unit, School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, United States

ARTICLE INFO

Keywords:
Milfoil
Widgeongrass
Root to shoot
Relative yield
Louisiana
Gulf of Mexico
Estuary

ABSTRACT

Submerged macrophyte habitats provide significant benefits to estuarine systems. In southeast Louisiana, *Myriophyllum spicatum* L. (milfoil) and *Ruppia maritima* L. (widgeongrass) are dominant species existing across fresh to brackish areas. Though frequently co-occurring across the range of salinity and light conditions, their individual responses to changing environmental conditions from restoration, weather and climate may determine overall species distribution, and biomass abundance. We compared milfoil and widgeongrass growth (i.e., biomass increase) across a range of salinity and light, in monoculture (salinity: 0, 5, 10, 15, 20; light: high ~ 50% ambient; low ~ 20% ambient), and in mixture (salinity: 0, 10, 20; light: high, low). In monoculture, milfoil growth was reduced at high salinity (20) versus low salinity (0), while biomass allocation differed significantly with greater allocation to shoots under high light, compared to low light. Widgeongrass was minimally affected by salinity, with reduced stem densities at high salinity compared to low salinity. In mixture, both species under-yielded compared to monoculture with milfoil reduced with high salinity and light, and low salinity and light; widgeongrass under-yielded with low salinity and high light, and mid salinity (10) and low light. These differences in species' responses suggest that salinity and light contribute to the distribution of milfoil and widgeongrass, with higher salinities and light favoring widgeongrass growth, and lower light possibly decreasing both species' growth, and ultimately, distribution. With continued changes occurring and predicted from both coastal restoration and climate change, understanding drivers of habitat forming species remains critical to inform future landscapes.

1. Introduction

Environmental gradients act as species filters, restricting community membership and defining habitats by creating selective environments that determine species distributions and biomass abundance (Austin, 1985; Weiher and Keddy, 1995). Along these gradients, interspecific interactions further shape communities (Keddy et al., 1998). Within estuarine systems, strong abiotic gradients largely driven by water clarity, nutrients, and salinity, often control species distributions through species' differential tolerances to environmental stressors (Kemp et al., 2004; Borgnis and Boyer, 2016). These abiotic responses may also be influenced by interspecific interactions, and their relative importance may vary across the abiotic gradients (Bertness and Shumway, 1993; Greiner La Peyre et al., 2001; Keddy, 1990). Management and restoration of estuarine communities, such as marshes and submerged macrophyte habitats, depend on understanding the critical drivers of key vegetation communities along these estuarine gradients.

Abundant and diverse submerged macrophyte communities exist across estuarine salinity gradients (Cerco and Moore, 2001; Hillmann et al., 2016; Shields and Moore, 2016). Species presence largely depends on favorable light conditions in water, such that enough light reaches the leaf area for photosynthesis and growth (Kemp et al., 2004; Koch, 2001). While light availability controls submerged macrophyte presence, community composition is often determined by both biotic and abiotic factors, including competition, salinity, substrate type, wave energy, inorganic carbon, and nutrients (Adair et al., 1994; Haller et al., 1974; Kemp et al., 2004; McCreary, 1991). Interactions of many of these biotic and abiotic variables have been shown to affect individual species differently, impacting growth rates, root to shoot ratio, growth morphology, and stem densities, ultimately influencing overall community composition and biomass abundance and distribution (Doyle and Smart, 2001; Gustafsson and Bostrom, 2011; McCreary,

* Corresponding author.
E-mail address: mlapeyre@agcenter.lsu.edu (M.K. La Peyre).

https://doi.org/10.1016/j.aquabot.2019.02.007
Received 26 October 2018; Received in revised form 19 February 2019; Accepted 25 February 2019
Available online 26 February 2019
0304-3770/ Published by Elsevier B.V.

1991; Shields et al., 2011; Shields and Moore, 2016; Zhu et al., 2008). Understanding the dominant factors controlling submerged macrophyte communities, including individual species' abundance and distribution, provides critical information to inform models predicting changes in habitat change and availability.

In estuaries in coastal Louisiana, environmental conditions are strongly controlled by riverine flows, which are largely related to precipitation, and the introduction of higher salinity Gulf waters from lunar tides, winds and storm events. The interaction of these influences results in salinity and water clarity gradients that control submerged macrophyte communities (Cho and Poirrier, 2005a; DeMarco et al., 2018; Hillmann et al., 2016; Merino et al., 2009). Salinity and light availability are predicted to change due to on-going and proposed restoration, river management, and climate change (e.g., Das et al., 2012; Wang et al., 2016). Proposed river diversions, which divert fresh riverwater and sediment into upper estuaries, may result in lowered salinity and increased turbidity across the estuarine gradient. Similarly, changes in precipitation patterns and storm events may alter the salinity gradient and impact water clarity within the estuaries. While a number of models predict changes to these environmental conditions, we still lack data to understand how submerged macrophyte species may respond, and the impacts on species distribution and availability of habitat.

Myriophyllum spicatum (Eurasian watermilfoil; hereinafter milfoil) and *Ruppia maritima* (widgeongrass) are ubiquitous and commonly co-occuring species dominating the submerged macrophyte communities from fresh to brackish estuarine waters in this region (Carter et al., 2009; Hillmann et al., 2016; Merino et al., 2009). Despite their common co-occurrence and overlapping ranges, these species are documented to have relatively different tolerances to key drivers, particularly salinity and light availability. For example, milfoil, a non-native, nuisance species, is described as a salt-tolerant freshwater species, adapted to low-light environments (Haller et al., 1974). Milfoil is generally reported as thriving in lower salinities, ranging from 0 to 10. A 2013–2015 survey of the northern Gulf of Mexico documented milfoil in areas with salinity ranging from 0 to 9.9, and across the range of photosynthically active radiation (PAR) recorded below surface waters (2.5–992.6 μmol m^{-2} s^{-1}; Hillmann et al., 2017). In contrast, widgeongrass is considered native and pervasive in aquatic environments in this region, and has been found in salinities from 0 to well over 50 (Kantrud, 1991). Within estuarine environments, widgeongrass has been reported to be limited by light availability, wave exposure and salinity variability (Adair et al., 1994; Bonis et al., 1993; Strazisar et al., 2015; Verhoeven, 1979), as well as by interspecific competition (Pulich and White, 1991; Verhoeven, 1979). Recent surveys in Barataria Basin, Louisiana found widgeongrass thriving in areas with salinity ranging from essentially 0 to 13 (Hillmann et al., 2017), and coastwide (Texas to Alabama) from essentially 0 to 24.1 (La Peyre et al., 2017). Understanding the interactions of co-occuring species along abiotic gradients enables better prediction of shifting submerged macrophyte habitats.

The response of milfoil and widgeongrass, representing over 50% of the estuarine submerged macrophyte community in this region (La Peyre et al., 2017), to changes in abiotic (salinity, light availability) gradients, alone and in mixture, may critically determine the availability and distribution of submerged macrophyte habitat in future landscapes in this region. This study examines the effects of competition on milfoil and widgeongrass on growth (i.e., biomass increase) in varying conditions of salinity and light. Specifically, this research examines: a) what effect will different salinity and light regimes have on milfoil and widgeongrass growing separately in monoculture, and b) how will the different treatments affect species interactions when plants are grown in mixture? This research provides critical information necessary to understand how submerged macrophyte habitat may shift over time across this landscape.

2. Methods

This experiment was conducted in an indoor greenhouse located at Louisiana State University Agricultural Center during the summer/fall of 2016. A factorial experiment of salinity (parts per thousand: 0, 5, 10, 15, 20), light intensity (50% ambient light, 20% ambient light), and species (milfoil, widgeongrass) in monoculture, and in mixture (at salinity of 0, 10, 20 and both light treatments), was used for a total of 26 treatment combinations. Each treatment combination was replicated three times for a total of 78 experimental units (pots; 10.0 cm diameter), which were placed into plastic, translucent tanks (0.7 m × 0.35 m × 0.4 m) in a completely randomized design. Specifically, the 78 experimental units (pots) were distributed among 30 tanks. Tanks were randomly assigned a salinity by light treatment and each treatment was replicated in 3 tanks. Three pots, each containing a single or multiple-species mixture (1 milfoil, 1 widgeongrass, 1 mixture) were placed in individual tanks, maintained at 0, 10, or 20 salinity (3 salinity treatments × 2 light treatments × 3 replicates = 18 tanks). Furthermore, two single species pots (1 milfoil, 1 widgeongrass) were placed in each of the 12 tanks with 5 and 15 salinity (2 salinity treatments × 2 light treatments × 3 replicates = 12 tanks).

Milfoil plants were collected in water depths of approximately 0.5 m from Fucich Bayou, LA, USA (29.504806, -89.668214; 1.0 salinity) and widgeongrass plants were collected in water depths of approximately 0.35 m from the northern shore of Lake Pontchartrain, Louisiana, USA, (30.261215, -89.956350; 3.0 salinity) on August 7 and 8, 2016. Sediment was also collected at both locations for use in the experiment. Plants and sediment were brought back to the Louisiana State University greenhouses in covered bins. Equal amounts of sediment from both sites were combined, homogenized and each pot was filled with approximately 450 ml of mixed sediment. One individual from a single species was planted in each monoculture pot and one individual of each species was planted in each mixture pot. For each species, one main shoot was placed in the required pots. Overall, for milfoil, a mean stem length of 8.20 cm ± 0.49 (mean ± SE), and stem density of 1.0 ± 0.0 were used. This stem density reflected stem densities recorded in field surveys (20 stems m^{-2}; unpubl. data). For widgeongrass, a mean stem length of 11.81 cm ± 0.21 (mean SE), and stem density of 8.95 ± 0.95 were used. This stem density reflected stem densities recorded in field surveys (180 stems m^{-2}; unpubl. results). A subset of 10 plants from each species was sampled and used to determine initial mean dry weight values (grams dry weight; g dw) as described below for dry weights (milfoil: 0.13 ± 0.03 g dw; widgeongrass: 0.07 ± 0.01 g dw).

After planting, the pots were randomly placed into tanks which were filled with tap water adjusted to a salinity of 10 using Instant Ocean Sea Salt (Instant Ocean, St. Blacksburg, VA), and to water temperatures controlled by ambient outdoor air temperature (range: 30–32 °C) as the greenhouses were not climate controlled. These water temperatures are reflective of local shallow water temperatures from where the species were collected. Pots were acclimated for 7 days prior to commencing the experiments. Starting on August 14, 2016, salinity was adjusted at a rate of 3 every 3 days until the target salinities were reached for each treatment. Treatments were randomly assigned to tanks prior to adjustments. Water levels were maintained at 3 cm below the top of the tank, approximately 15 cm above the top of the pot. Experiments were initiated on August 26, 2016 and run for 8 weeks. The greenhouse was constructed of glass panels and the light source used in this experiment was natural light coming through the glass panels of the greenhouse. Light intensity (photosynthetically active radiation, PAR; μmol m^{-2} s^{-1}) was monitored weekly throughout the experiment using a light intensity meter (LI-1400 LI-COR, NE). We measured ambient light in the greenhouse (ambient) and light under the water surface (~5 cm below surface) in the experimental tanks. A neutral density (50% light reduction) shade cloth was placed over the top of the low light treatment tanks. The low light treatment tanks

maintained ~20% ambient light throughout the experiment. No shade cloths were used on the high light treatment tanks, which maintained ~50% ambient light conditions. The 50% ambient light condition for high light was due to attenuation from the greenhouse. On the first day of the experiment, all stem lengths (cm), and stem densities (#) were measured for each pot and recorded. Throughout the experiment, salinity, temperature (°C), and dissolved oxygen (mg L^{-1}) were monitored every 3 days using a handheld YSI 6000 (Yellow Springs Instrument, Inc.). Salinity and water levels were adjusted as needed to maintain treatment target values.

At the end of the experiment, all plant material was harvested and brought to the lab for measurements of stem length, stem density, and aboveground and belowground biomass. Biomass was determined by drying the plants at 60^0C until a constant weight was obtained (g dw). Total growth rate was based on dry weights of total biomass (aboveground biomass + belowground biomass). The average initial dry weight values calculated for each species were subtracted from final dry weight values and divided by the number of days in the experiment (g dw day^{-1}). Root to shoot ratio was determined by dividing the belowground biomass (g) by the aboveground biomass (g). Stem length growth rate was determined by subtracting initial stem lengths from final stem lengths and dividing by the number of days in the experiment (cm day^{-1}). Stem density was determined at the end of the experiment by visually counting the number of vertical stems ascending from roots.

Interaction between species was analyzed by calculating relative yielding; relative yield totals were used to determine species complementarity (an overall increase in productivity of bi-cultures compared to monocultures; Hooper, 1998; Shields and Moore, 2016). Relative yielding was determined by first calculating the expected mean of the total growth rate for each species in monoculture across all treatments and treatment combinations. Next, the total growth rate of each species in mixture was calculated and this value was divided by the expected mean in monoculture, resulting in a ratio of yielding in monoculture versus bi-culture. Over-yielding occurs when a species' relative yielding > 1; under-yielding occurs when relative yielding < 1 (Shields and Moore, 2016). When relative yield totals > 1, species are considered complementary as long as each species has an individual relative yielding > 1 (Gustafsson and Bostrom, 2011; Shields and Moore, 2016).

For all tests a significance value of $p < 0.05$ was used. Data were tested for assumptions of normality (Shapiro–Wilk test statistic) and homogeneity of variance, and transformations applied as needed. Analyses of variance (ANOVA) was run for both species separately in monoculture for total growth rate (i.e., biomass increase, g dw day^{-1}), root to shoot ratio (g g^{-1}), stem density, and stem length growth rate (cm day^{-1}), with salinity and light as fixed factors, and tank as a random effect. Tukey's HSD tests were run when significant differences were found. Two-sample t-tests were run on total growth rate means of species in mixture and monoculture to determine whether species relative yielding and relative yield totals differed significantly from 1. All data analyses were performed in SAS 9.4 (SAS Institute Inc., 2013). Mean and standard error are reported unless indicated otherwise.

3. Results

3.1. Environmental conditions

Salinity treatments remained consistent with target salinities. Mean measured ambient light inside the greenhouse throughout the experiment was 731.6 ± 132.0 µmol m^{-2} s^{-1}. Mean high light in the experimental tanks was 353.6 ± 124.2 µmol m^{-2} s^{-1} (~50% of ambient light) and mean low light was 150.0 ± 47.4 µmol m^{-2} s^{-1} (~20% of ambient light; Table 1). Mean temperature did not differ among tanks, or days of the experiment (31.7 ± 0.10^0C).

3.2. Individual species response in monocultures

Salinity and light significantly affected milfoil growth, with no significant interactive effects (Fig. 1, Table 2). Total growth rate was greater at a salinity of 0, compared to all other salinities which did not differ. Milfoil stem density and stem length growth rate were also greater at a salinity of 0, but only compared to higher salinities of 15 and 20. Total growth rate and root to shoot ratio were significantly greater under the high light as compared to the low light treatment.

Widgeongrass growth was not affected by light, or the interaction of light and salinity (Table 2). Salinity had a significant impact on widgeongrass stem density, with greater stem density at 0 compared to 20. Neither light, nor the interaction of salinity and light had a significant effect on widgeongrass growth.

3.3. Relative yield

Under conditions of high light, milfoil under-yielded at high salinity (20), while widgeongrass under-yielded at low and mid salinity (0, 10; Fig. 2). Under conditions of low light, milfoil under yielded at low and mid salinity (0, 10), while widgeongrass also under-yielded at mid-salinity (10). In both high and low light, overall relative yield totals did not differ significantly from 1, and never had all relative yields > 1, suggesting no complementarity.

4. Discussion

Both species displayed a wide tolerance to the tested salinity and light conditions supporting their ubiquitous presence across the fresh to brackish estuarine gradient. Differences in milfoil and widgeongrass response to both salinity and light however suggest impacts to species biomass, abundance and distribution across the estuarine gradient with changing conditions. Specifically, while widgeongrass growth (biomass) in monoculture was not significantly affected by salinity or light conditions, milfoil growth (biomass) in monoculture was significantly reduced with increasing salinity and reduced light conditions. Overall species performance of both species in mixture was similar to that in monoculture suggesting that the abiotic gradients of salinity and light are more important in controlling these species' distributions in this estuarine setting.

Both salinity and light had significant impacts on milfoil growth and biomass allocation, suggesting this species' distribution will be limited by increased salinities, while adapting to some extent to lower light through changes in biomass allocation. Specifically, milfoil growth decreased as salinity increased, however allocation, as measured by root to shoot ratio, was impacted by light availability. Reduced light availability resulted in changes in biomass allocation with more investment in aboveground biomass under low light conditions. This root to shoot ratio difference was detected at 20% ambient light (~150 µmol m^{-2} s^{-1}) although past studies have shown milfoil growing in 1–2% ambient light (~ < 10 µmol m^{-2} s^{-1}; Grace and Wetzel, 1978), which matches observations from Louisiana where milfoil grew in 2.52–992.6 µmol m^{-2} s^{-1} (Hillmann et al., 2017). Understanding biomass allocation in milfoil along light gradients provides insight into how this species adapts to changing conditions, and how milfoil may respond to periods or conditions of low light. These results are consistent with other studies that show high milfoil abundance in low light (Zhu et al., 2008), suggesting an advantage over other species in turbid waters, such as within disturbed and changing coasts, and deltaic environments.

Salinity and light are often highlighted as the two dominant abiotic factors restricting widgeongrass growth (Adair et al., 1994; Bonis et al., 1993; Moore et al., 2014; Pulich, 1985; Strazisar et al., 2015; Verhoeven, 1979) despite the species tolerance to a wide range of both factors (Kantrud, 1991). Recent surveys along the northern Gulf of Mexico found widgeongrass growing across the salinity gradient and

Table 1
Recorded environmental conditions. All values reported as means ± SE. Ambient light represents atmospheric light measured inside greenhouse; high light represents light just below surface water in tanks (5 cm) with no shade cloth; low light represents light just below surface water (5 cm) in tanks with shade cloth.

	Salinity				
	0	5	10	15	20
Salinity	0.91 ± 0.21	5.21 ± 0.06	10.14 ± 0.08	15.09 ± 0.09	19.86 ± 0.23
DO (mg L^{-1})	7.57 ± 0.263	6.51 ± 0.19	6.14 ± 0.17	5.48 ± 0.12	5.20 ± 0.12
temperature (°C)	31.6 ± 0.23	31.57 ± 0.22	31.85 ± 0.23	31.73 ± 0.23	31.74 ± 0.23

	Light		
	ambient	high	low
PAR (μmol m^{-2} s^{-1})	731.6 ± 132.0	353.6 ± 124.2	150.0 ± 47.4

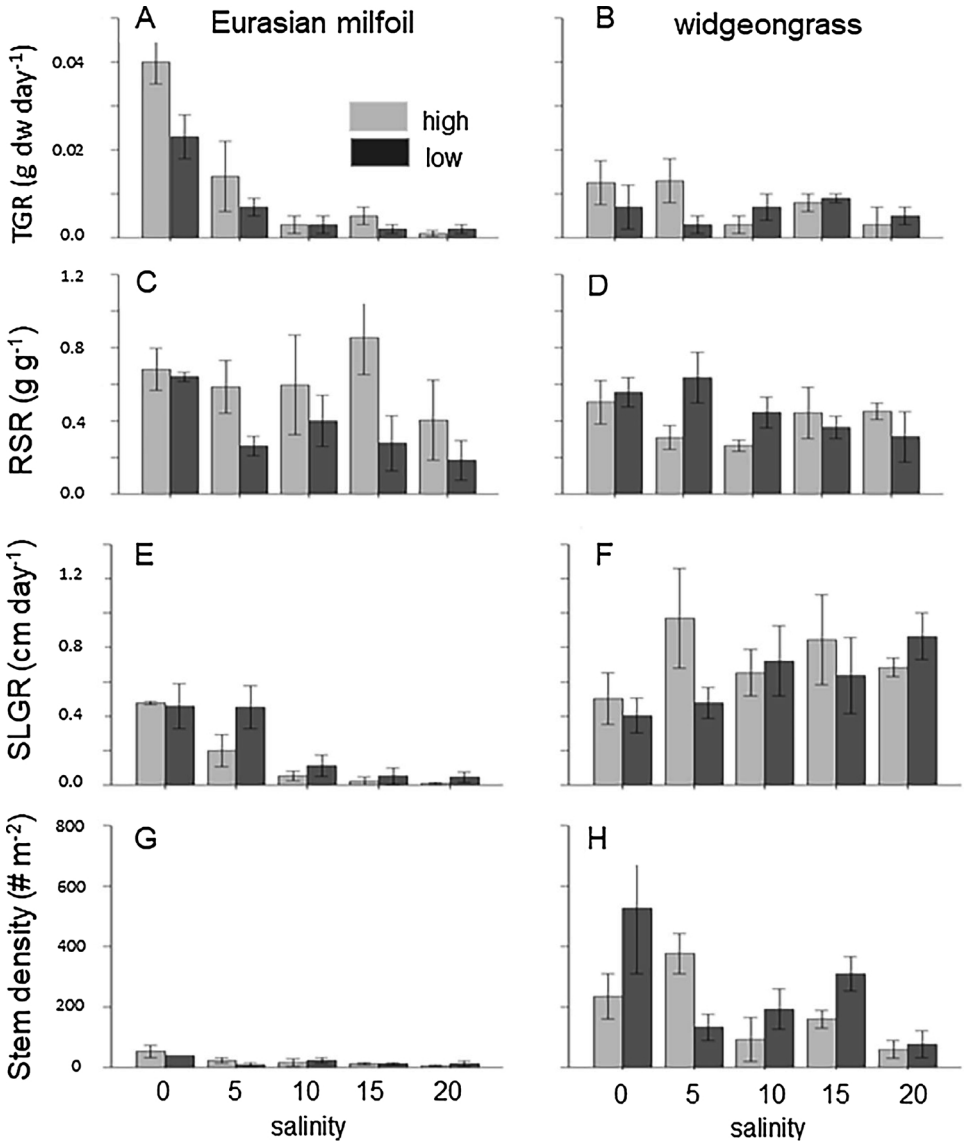

Fig. 1. Total growth rate (TGR; g dw day^{-1}), root to shoot ratio (RSR; g g^{-1}), stem length growth rate (SLGR; cm day^{-1}) and stem density (# m^{-2}) of Eurasian milfoil (left panels A, C, E, G) and widgeongrass (right panels B, D, F, H) in monoculture across all salinity (0, 5, 10, 15, 20) and light treatments (high light: light grey ~ 50% ambient; low light; dark grey ~20% ambient). Values are means ± 1 SE, n = 3. Significant differences are indicated in Table 2.

was one of only a few species in brackish and saline areas (Hillmann et al., 2016). In this greenhouse study, widgeongrass was minimally affected by either salinity or light. The salinity and light range tested were well within the reported range for wideongrass (Kantrud, 1991; Kemp et al., 2004). Widgeongrass however may be more affected by variation, or extremes of controlling abiotic factors. For example, pulses of freshwater have previously been shown to decrease widgeongrass growth rates (La Peyre and Rowe, 2003).

Table 2
Two-way ANOVA was used to test the effects of salinity and light, and the interaction of salinity and light on Eurasian milfoil and widgeongrass total growth rate (g dw day^{-1}), root to shoot ratio (g g^{-1}), stem density (# m^{-2}) and stem length growth rate (cm day^{-1}) for each species in monoculture. For each test a significance value of p = 0.05 was used. Significant results (p < 0.05) are bolded below.

		Total Growth Rate		Root to Shoot Ratio		Stem Density		Stem Length Growth Rate	
	DF	F	p	F	p	F	p	F	p
Eurasian milfoil									
light	1	**4.44**	**0.048**	**7.33**	**0.0139**	0.11	0.7439	3.47	0.0774
salinity	4	**22.57**	**< 0.0001**	1.51	0.2372	**5.01**	**0.0053**	**15.55**	**< 0.0001**
salinity * light	4	1.68	0.1947	1.64	0.2028	0.75	0.5696	0.94	0.4604
Residual	20								
widgeongrass									
light	1	0.93	0.3464	1.77	0.1982	0	0.9871	0.94	0.3439
salinity	4	0.99	0.4359	1.57	0.2213	**3.34**	**0.0163**	1.02	0.4227
salinity * light	4	1.68	0.193	1.1	0.3839	0.69	0.6067	1.05	0.4049
Residual	20								

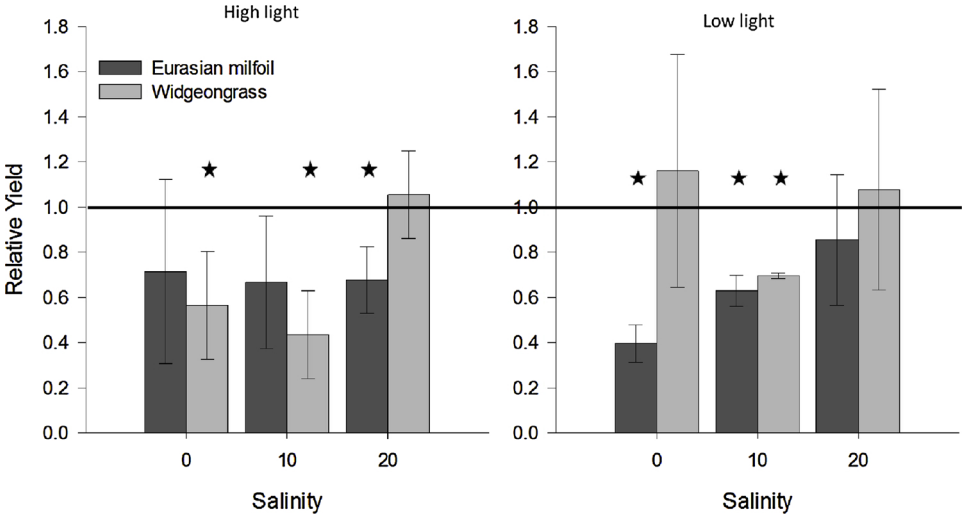

Fig. 2. Relative yield calculated based on total growth rate (TGR; g dw day^{-1}) for Eurasian milfoil and widgeongrass for three salinity (0, 10, 20) and light (high, low) treatment combinations. High light treatment on left panel, low light treatment on right panel. Values are means ± 1 SE, n = 3. A line is drawn across a relative yield of 1 which represents species performing equally well in mixture compared with monoculture. Stars indicate significant under (< 1) yielding (Student's t-test; p < 0.05).

Studies examining widgeongrass and light have yielded inconsistent results, with widgeongrass at times performing better with high light (Cho and Poirrier, 2005a), but also tolerating frequent periods of increased turbidity (Kantrud, 1991). In this study, we targeted the observed average high (353.58 ± 124.21 µmol m^{-2} s^{-1}) and low light (149.99 ± 47.41 µmol m^{-2} s^{-1}) conditions previously recorded at submerged macrophyte bed water bottoms for this area, but did not capture the high and low ends of the observed range (range: 2.52–992.6 µmol m^{-2} s^{-1}; unpubl. results). Past field studies found differences in growth rates when the lower and higher limits of light availability were tested (Kemp et al., 2004). It may be that variation or extremes of abiotic factors are more important in controlling widgeongrass.

Along abiotic gradients, interspecific interactions may also alter outcomes. In this study, under high light conditions, widgeongrass under-yielded at low salinities (0, 10) while milfoil under-yielded at the high salinity (20), suggesting potential competitive effects that may be driven by salinity, when light is not limiting. In contrast, under low light conditions, significant effects were found only at low salinities, with both species significantly under-yielding at the mid-salinity (10) treatment. Density-dependent impacts related to the initial experimental design may be why no species significantly over-yielded (Roush et al., 1989). Specifically, this study examined competition at densities of 20 stems m^{-2} (milfoil) and 180 stems m^{-2} (widgeongrass), which is typical within these habitats. At the species and assemblage level, some research has shown a negative correlation between submerged macrophyte stem density and growth and biomass allocation of co-occurring species (Wolfer and Straile, 2004). While these findings were generated in a study using higher initial stem densities than this study, the suggestion is that initial low starting densities may result in a failure to reach density thresholds necessary to expose negative density dependent relationships between plant species. In our study the initial starting density for both species were within the reported range observed across the salinity gradient for these species. However, widgeongrass can reach stem densities that far exceed the initial conditions of this study (Kantrud, 1991), and therefore it was difficult to identify a critical density threshold. Future studies may want to consider using multiple starting densities.

Greenhouse competition experiments examine only interactions between already established plants. In interpreting these results and extrapolating to the field, it is important to understand how the individual species spread and establish. For example, past studies suggest that milfoil thrives through its ability to spread easily through fragmentation (Smith et al., 1991; Zhu and Georgian, 2014). Its competitive ability appears linked to dispersal method, biomass allocation and timing of recruitment into communities (Smith et al., 1991). Within established beds of native submerged macrophytes, milfoil production is often depressed, failing to outcompete existing species (Madsen et al., 1995). Widgeongrass expansion has been hypothesized to be a result of its ability to tolerate broad salinity and light gradients and its ability to colonize rapidly through sexual and asexual reproduction (Cho and Poirrier, 2005b; Cho et al., 2009; Johnson et al., 2003; Strazisar et al., 2015). For example, in high salinity areas with frequent disturbances, widgeongrass has replaced seagrass species such as *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme* and *Zostera marina* (Cho et al., 2009; Johnson et al., 2003). One study in southeast Louisiana

documented rapid increases in widgeongrass during periods of La Niña, which bring higher salinity and water clarity (Cho and Poirrier, 2005b). Under the conditions tested, milfoil growth was reduced by the presence of widgeongrass, but only at high salinity (20) and high light, and low salinity (0, 10) and low light. Although this work does not address dispersal and recruitment, a reasonable conclusion from the data would suggest that environmental changes resulting in increasing salinity and light may favor widgeongrass over milfoil, while conditions of decreasing light availability might ultimately reduce growth of both species.

Differences in species responses to both salinity and light suggest that these two factors contribute significantly to the distribution of milfoil and widgeongrass. With continued changes in estuarine conditions of salinity and light across coastal Louisiana (Das et al., 2012; Wang et al., 2016) due to climate change, human disturbance and restoration activities, changes in submerged macrophyte habitat availability and species composition are likely to occur. In particular, two dominant species, milfoil and widgeongrass, may be differentially impacted by these changing abiotic conditions, with higher salinities and light favoring widgeongrass growth, and lower light levels possibly decreasing both species' growth, and ultimately, distribution. Decreased submerged macrophyte habitat affects faunal species (i.e. waterfowl, fish, invertebrates) by reducing habitat complexity, reducing refuge areas and food resources (Bortolus et al., 1998; Kanouse et al., 2006; La Peyre and Gordon, 2012; Poirrier et al., 2009; Valinoti et al., 2011; Wicker and Endres, 1995). Understanding the critical environmental drivers of submerged macrophytes provides for better estimations of changing submerged macrophyte biomass abundances and distribution.

Conflicts of interest

The authors declare that we have no significant competing financial, professional, or personal interests that may have influenced the performance or presentation of the work contained in this manuscript.

Author contributions

ERH, MKL contributed to idea development. ERH collected data, processed samples and managed all daily activities. ERH, MKL analyzed data. ERH, MKL contributed to manuscript writing.

Declarations of interest

None.

Acknowledgments

This work was supported by funding provided through a grant to MKL from the U.S. Department of Interior, U.S. Geological Survey, South Central Climate Science Center. Data are provided in Supplementary Table 1. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank Katie Bowes for assistance with collecting plants and maintaining the greenhouse experiment. We thank Dr. M. Poirrier, and 3 anonymous reviewers for comments that improved this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.aquabot.2019.02.007.

References

Adair, S.E., Moore, J.L., Onuf, C.P., 1994. Distribution and status of submerged vegetation in estuaries of the upper Texas coast. Wetlands 14, 110–121. https://doi.org/10.1007/BF03160627.

Austin, M.P., 1985. Continuum concept, ordination methods and niche theory. Annu. Rev. Ecol. Evol. Syst. 16, 39–61. https://doi.org/10.1146/annurev.es.16.110185.000351.

Bertness, M.D., Shumway, S.W., 1993. Competition and facilitation in marsh plants. Amer. Nat. 142, 718–724.

Bonis, A., Grillas, P., van Wijck, C., Lepart, J., 1993. The effect of salinity on the reproduction of coastal submerged macrophytes in experimental communities. J. Veg. Sci. 4, 461–468. https://doi.org/10.2307/3236073.

Borgnis, E., Boyer, K.E., 2016. Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the upper San Francisco estuary. Estuaries Coasts 707–717. https://doi.org/10.1007/s12237-015-0033-5.

Bortolus, A., Iribarne, O.O., Martinez, M.M., 1998. Relationship between waterfowl and the seagrass *Ruppia maritima* in a southwestern Atlantic coastal lagoon. Estuaries 21, 710–717.

Carter, J., Merino, J.H., Merino, S.L., 2009. Mesohaline submerged aquatic vegetation survey along the U.S. Gulf of Mexico coast, 2000: a stratified random approach. Gulf Mex. Sci. 1, 1–8.

Cerco, C.F., Moore, K., 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. Estuaries 24, 522–534.

Cho, H.J., Poirrier, M.A., 2005a. Seasonal growth and reproduction of *Ruppia maritima* L. s.l. in Lake Pontchartrain, Louisiana, USA. Aquat. Bot. 81, 37–49. https://doi.org/10.1016/j.aquabot.2004.10.002.

Cho, H.J., Poirrier, M.A., 2005b. Response of submersed aquatic vegetation (SAV) in Lake Pontchartrain, Louisiana to the 1997–2001 El Nino southern oscillation shifts. Estuaries 28, 215–225.

Cho, H.J., Biber, P., Nica, C., 2009. The rise of Ruppia in seagrass beds: changes in coastal environment and research needs. In: Drury, E.K., Pridgen, T.S. (Eds.), Handbook on Environmental Quality. Nova Science Publishers, Inc., pp. 1–15.

Das, A., Justic, D., Inoue, M., Hoda, A., Huang, H., Park, D., 2012. Impacts of Mississippi River diversions on salinity gradients in a deltaic Louisiana estuary: ecological and management implications. Estuar. Coast. Shelf Sci. 111, 17–26. https://doi.org/10.1016/j.ecss.2012.06.005.

DeMarco, K., Couvillion, B., Brown, S., La Peyre, M., 2018. Submerged aquatic vegetation mapping in coastal Louisiana through development of a spatial likelihood occurrence (SLOO) model. Aquat. Bot. 151, 87–97.

Doyle, R.D., Smart, M., 2001. Impacts of water column turbidity on the survival and growth of *Vallisneria americana* winterbuds and seedlings. J. Lake Reserv. Manag. 17, 17–28. https://doi.org/10.1080/07438140109353969.

Grace, J.B., Wetzel, R.G., 1978. The production biology of eurasian milfoil (*Myriophyllum spicatum L.*): a review. J. Aquat. Plant Manage. 16, 1–11.

Greiner La Peyre, M.K., Grace, J.B., Hahn, E., Mendelssohn, I.A., 2001. The importance of competition in regulating plant species abundance along a salinity gradient. Ecology 82, 62–69.

Gustafsson, C., Bostrom, C., 2011. Biodiversity influences ecosystem functioning in aquatic angiosperm communities. Oikos 120, 1037–1046. https://doi.org/10.1111/j.1600.

Haller, W.T., Sutton, D.L., Barlowe, W.C., 1974. Effects of salinity on growth of several aquatic macrophytes. Ecology 55, 891–894.

Hillmann, E.R., DeMarco, K.E., La Peyre, M., 2016. Establishing a baseline of estuarine submerged aquatic vegetation resources across salinity zones within coastal areas of the northern Gulf of Mexico. J. Southeast. Assoc. Fish Wildl. Agencies 3, 25–32.

Hillmann, E., DeMarco, K., La Peyre, M.K., 2017. Submerged Aquatic Vegetation and Environmental Data Along A Salinity Gradient in Barataria Bay, Louisiana (2015). U.S. Geological Survey Data Releasehttps://doi.org/10.5066/F7M61HG4.

Hooper, D.U., 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecol. Lett. 79, 704–719.

Johnson, M.R., Williams, S.L., Lieberman, C.H., Solbak, A., 2003. Changes in the abundance of the seagrasses *Zostera marina L.* (eelgrass) and *Ruppia maritima* L. (widgeongrass) in San Diego, California, following an El Nino event. Estuaries 26, 106–115.

Kanouse, S., La Peyre, M., Nyman, J., 2006. Nekton use of *Ruppia maritima* and non-vegetated bottom habitat types within brackish marsh ponds. Mar. Ecol. Prog. Ser. 327, 61–69. https://doi.org/10.3354/meps327061.

Kantrud, H.A., 1991. Widgeongrass (*Ruppia maritima*): a literature review. Fish Wildl. Res. 10.

Keddy, P.A., 1990. Competitive hierarchies and centrifugal organization in plant communities. In: Grace, J.B., Tilman, D. (Eds.), Perspectives on Plant Competition. Academic Press, San Diego, CA, USA, pp. 265–290.

Keddy, P.A., Fraser, L.H., Wisheu, I.C., 1998. A comparative approach to examine competitive response of 48 wetland plant species. J. Veg. Sci. 9, 777–786.

Kemp, M.W., Batleson, R., Bergstrom, P., Carter, V., Gallegos, C.L., Hunley, W., Karrh, L., Koch, E.W., Landwehr, J.M., Moore, K.A., Murray, L., Naylor, M., Rybicki, N.B., Stevenson, J.C., Wilcox, D.J., 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. Estuaries 27, 363–377. https://doi.org/10.1007/BF02803529.

Koch, E.W., 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24, 1–17.

La Peyre, M.K., Gordon, J., 2012. Nekton density patterns and hurricane recovery in submerged aquatic vegetation, and along non-vegetated natural and created edge habitats. Estuar. Coast. Shelf Sci. 98, 108–118. https://doi.org/10.1016/j.ecss.2011.12.010.

La Peyre, M.K., Rowe, S., 2003. Effects of salinity changes on growth of *Ruppia maritima* L. Aquat. Bot. 77, 235–241. https://doi.org/10.1016/S0304-3770(03)00109-8.

La Peyre, M., DeMarco, K., Hillmann, E.R., 2017. Submerged Aquatic Vegetation and Environmental Data for Coastal Areas From Texas through Alabama, 2013–2015. U.S.

Geological Survey data releasehttps://doi.org/10.5066/F7GH9G44.
Madsen, J.D., Smart, R.M., Dick, G.O., Honnell, D.R., 1995. The influence of an exotic submersed aquatic plant, *Myriophyllum spicatum*, on water quality, vegetation, and fish populations of Kirk Pond, Oregon. Engineers, U.S.A.C. of (Ed.), 29th Annual Meeting, Aquatic Plant Control Research Program pp. 329.
McCreary, N.J., 1991. Competition as a mechanism of submersed macrophyte community structure. Aquat. Bot. 41, 177–193. https://doi.org/10.1016/0304-3770(91)90043-5.
Merino, J.H., Carter, J., Merino, S.L., 2009. Mesohaline submerged aquatic vegetation survey along the U.S. Gulf of Mexico coast, 2001 and 2002: a salinity gradient approach. Gulf Mex. Sci. 1, 9–20.
Moore, K.A., Shields, E.C., Parrish, D.B., 2014. Impacts of episodic climatic events on *Zostera marina* (eelgrass) and its interactions with *Ruppia maritima* (widgeon grass). Estuaries Coasts 37, 30.
Poirrier, M.A., Spalding, E.A., Franze, C.D., 2009. Lessons learned from a decade of assessment and restoration studies of benthic invertebrates and submersed aquatic vegetation in Lake Pontchartrain. J. Coast. Res. 54, 88–100.
Pulich, W.M., 1985. Seasonal growth dynamics of *Ruppia* maritima L. and *Halodule wrightii* aschers in southern Texas and evaluation of sediment fertility status. Aquat. Bot. 23, 53–66.
Pulich, W.M., White, W.A., 1991. Decline of submerged vegetation in the Galveston Bay system: chronology and relationships to physical processes. J. Coast. Res. 7, 1125–1138.
Roush, M.L., Radosevich, S.R., Wagner, R.G., Maxwell, B.D., Petersen, T.D., 1989. A comparison of methods for measuring effects of density and proportion in plant competition experiments. Weed Sci. 37, 268–275.
SAS Institute Inc, 2013. Base SAS® 9.4 Procedures Guide. SAS Institute Inc., Cary, NC.
Shields, E.C., Moore, K.A., 2016. Effects of sediment and salinity on the growth and competitive abilities of three submersed macrophytes. Aquat. Bot. 132, 24–29. https://doi.org/10.1016/j.aquabot.2016.03.005.
Shields, E.C., Moore, K.A., Parrish, D.B., 2011. Influences of salinity and light availability on abundance and distribution of tidal freshwater and oligohaline submersed aquatic vegetation. Estuaries Coasts 35, 515–526. https://doi.org/10.1007/s12237-011-9460-0.
Smith, C.S., Barko, J.W., Mcfarland, D.G., 1991. Ecological considerations in the management of Eurasian watermilfoil in Lake Minnetonka, Minnesota. Technical Report A-91-3. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, Mississippi.
Strazisar, T., Koch, M.S., Madden, C., 2015. Seagrass (*Ruppia maritima L.*) life history transitions in response to salinity dynamics along the Everglades-Florida Bay. Estuaries Coasts 38, 337–352. https://doi.org/10.1007/s12237-014-9807-4.
Valinoti, C.E., Ho, C., Armitage, A.R., 2011. Native and exotic submerged aquatic vegetation provide different nutritional and refuge values for macroinvertebrates. J. Exp. Mar. Bio. Ecol. 409, 42–47. https://doi.org/10.1016/j.jembe.2011.08.001.
Verhoeven, J.T.A., 1979. The ecology of Ruppia-dominated communities in western Europe. I. Distribution of Ruppia representatives in relation to their autoecology. Aquat. Bot. 6, 197–267.
Wang, H., Chen, Q., Hu, K., La Peyre, M.K., 2016. A modeling study of the impacts of the proposed Mississippi River Diversion and sea level rise on water quality of a deltaic estuary. Estuaries Coasts. https://doi.org/10.1007/512237-016-0197-7.
Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. OIKOS 73, 323–335.
Wicker, A.M., Endres, K.M., 1995. Relationship between waterfowl and American Coot abundance with submersed macrophytic vegetation in Currituck Sound, North Carolina. Estuaries 18, 428–431. https://doi.org/10.2307/1352325.
Wolfer, S.R., Straile, D., 2004. Density control in *Potamogeton perfoliatus* L. and *Potamogeton pectinatus* L. Limnologica 34, 98–104. https://doi.org/10.1016/S0075-9511(04)80027-6.
Zhu, B., Georgian, S.E., 2014. Interactions between invasive Eurasian watermilfoil and native water stargrass in Cayuga Lake, NY, USA. J. Plant Ecol. 7, 499–508. https://doi.org/10.1093/jpe/rtt063.
Zhu, B., Mayer, C.M., Rudstam, L.G., Mills, E.L., Ritchie, M.E., 2008. A comparison of irradiance and phosphorus effects on the growth of three submerged macrophytes. Aquat. Bot. 88, 358–362. https://doi.org/10.1016/j.aquabot.2008.01.003.